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Noteworthy for Managers

Randall Brown

Here are two examples of programs of possible interest to Interagency Program staff and management.

CVPIA Fish Team

Over the past several weeks a small team of biologists has been grappling with nine actions proposed by the Department of Interior to help increase populations of several anadromous fish using the Sacramento/San Joaquin estuary. Team members include Wim Kimmerer, Marty Kjelson, Roger Guinee, Jim White, Terry Mills, Ken Lentz, Gary Stern, Elise Holland, Chuck Hanson, Serge Birk, Pete Rhoads, and me.

Although the team has made progress defining the actions and designing many of them in the form of tests to better evaluate their contribution to species recovery, there has not been complete agreement on their scientific underpinnings. At the October 8 meeting, the team discussed a process to clarify our understanding of the science behind these and other management actions to protect and enhance fish populations. We agreed that the Interagency Program (perhaps in cooperation with the Modeling Forum) will sponsor one or more workshops to examine X_2 as a management tool. The workshop(s) will probably be held early in 1998. Although we generally agreed to the need for similar evaluations of striped bass and salmon data, we did not agree on a process. Some team members recommended that the Interagency Program conduct these evaluations, but others were not convinced that this was the best forum.

Watershed Protection and Restoration Council

On July 31, 1997, Governor Pete Wilson created the Watershed Protection and Restoration Council, which will be responsible for oversight of State activities to protect and enhance watersheds and the conservation and restoration of anadromous salmonids in California. The council will have a working group (consisting of agency directors and executive officers of Northern California regional water quality control boards and chaired by the SWRCB Executive Officer), a science panel, and three advisory committees. A general program goal it develop a program of California conservation actions that will allow the National Marine Fisheries Service to promulgate a rule that, in effect, allows California to manage the recovery of federally listed anadromous salmonids such as steelhead and coho.

The Watershed Protection and Restoration Council may have direct and indirect effects on the Interagency Program. One direct effect is that Jerry Johns (SWRCB) is deeply involved in the working group and will have less time to devote to IEP activities. The program also includes a requirement to develop a list of recovery and monitoring activities that can protect and conserve anadromous salmonid resources. In the bay/delta and Central Valley, the monitoring could complement existing Interagency Program elements.

Flow Effects and Density Dependence in Striped Bass

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Among the numerous challenges facing fisheries scientists are determining causes of long-term trends, assessing environmental effects on populations, and detecting compensatory mechanisms within populations. This report summarizes some of the analyses I have recently conducted to investigate these issues with regard to striped bass in the San Francisco estuary.

Two features of the bay/delta striped bass population are well known: the influence of freshwater flow and diversions on abundance or survival of young, and the long-term decline. The effects of flow during early development on abundance of adult striped bass is evident in data going back to the 1930s (Stevens 1977). Effects on young bass of outflow (Turner and Chadwick 1972) and export flow (Chadwick *et al* 1977) have also been known for a considerable time. Although the mechanism for effects of exports is obvious, that for flow is not. Proposed mechanisms for increased young survival with increased flow include variation of spawning time, inputs of nutrients or organic matter, dilution of toxic substances, reduced settlement of eggs, turbidity effects on visual predation on young bass, and transport to favorable feeding grounds (Turner and Chadwick 1972; Stevens *et al* 1985).

Explanations for the long-term decline have also varied, but in recent years export flows, and consequent entrainment of young fish, have been advanced as the principal cause of the decline (DFG 1987). Although adult mortality has increased during that time as well, the principal mechanism for the decline has been reported as a positive feedback between entrainment, reduced recruitment, subsequently reduced adult abundance

and egg supply, resulting ultimately in still lower young-of-the-year abundance. Bennett and Howard (this issue) offer an alternative explanation: migration of older adults to the ocean has increased since 1977 as a response to generally warmer sea surface temperature, and this migration has reduced the abundance of older, more fecund adults and therefore the egg supply.

Any fish population must have at least one compensatory mechanism to support a sustainable fishery. Compensatory mechanisms or density dependence are most often detected as saturating functions describing the relationship between two successive life stages (most often stock size and recruitment). In the case of a stock-recruit curve, as the spawning stock increases recruitment increases initially, then either levels off (Beverton-Holt curve) or begins to decline (Ricker curve). In either case, there is a restriction in the life cycle that limits the total number of recruits around a maximum called the "carrying capacity". Density dependence may also be detected as a negative relationship between abundance and growth rate, or, less frequently, between abundance and survival or mortality. In the latter case, density dependence is indicated by mortality that increases with increasing population size.

In this report, I present several analyses and draw several conclusions about the decline, the influence of flow and exports, and the effect of density dependence. In contrast to the analyses reported by Bennett and Howard (this issue), I examined only data from within the estuary, and focused mainly on conditions leading up to recruitment at age 3.

Analyses

Striped bass are long-lived and can reproduce repeatedly. Analyses relating abundance of this population to environmental conditions can encounter difficulties with autocorrelation, and results can be difficult to interpret because of the feedback through the life cycle. Therefore I analyzed survival indices (ratios of abundance indices of successive life stages) or mortality (time rates of change of abundance).

Space does not permit a complete exposition of the data used or analyses performed. Briefly, I used a variety of data for various segments of the life cycle of striped bass. These included data on abundance of adults (catch-per-effort data or Petersen estimates based on mark/recapture), adult mortality (based on tag returns), fecundity, abundance of eggs and larvae, and abundance indices and raw data from summer tow-net, fall midwater trawl, San Francisco Bay study, and salvage sampling.

Data analyses focused on the relationship of abundance and survival to flow and evidence for density dependence. Most of the analyses comprised linear regression, in some cases using modern techniques such as robust or tree regression (Venables and Ripley 1994). The analysis was based on explorations of the data using various graphical techniques. Regression and other analyses are reported only if examination of plots of residuals revealed that the assumptions underlying the regression methods were met.

Time Trends

The time course of abundance of adults (Figure 1) reveals three key features. First, all age classes have de-

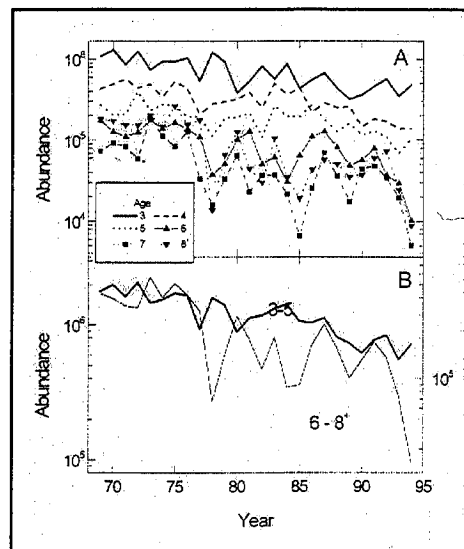


Figure 1. Time course of Petersen mark/recapture estimates of abundance of striped bass adults by age-class. A, by age class; B, grouped age classes 3-5 years (heavy line, left axis) and 6 years and over (thin line, right axis), scaled so the mean of values before 1978 overlies each other.

clined in abundance. Second, the pattern of decline is different for age classes 3-5 and 6 and older: younger fish have declined at a nearly constant rate, while older fish declined sharply on several occasions, particularly 1977-78 and 1993-94 (Figure 1B). Third, the sharp declines in abundance of the older fish are not preceded by similar declines of younger fish in previous years. If the decline had been caused by recruitment failure, we would see a decline first in age 3, then age 4 the next year, and so forth. Since we do not see this pattern, the Petersen abundance estimates do not support a conclusion that loss of young fish in the early 1970s caused a recruitment failure later. However, the observed pattern is consistent with the mechanism proposed by Bennett and Howard (this issue).

Adult mortality estimated from angler tag returns has increased over time (DFG 1987) (robust linear regression, $p=0.001$). Estimates of mortality by year-class based on Pe-

tersen abundance estimates had a significant step increase in year-class 1969-1970 (robust regression, $p=0.009$), corresponding roughly to the sharp decreases in abundance of older fish in 1977-78. Both of these results suggest that adults are not surviving as well as they did in the 1960s. This increase in mortality has undoubtedly contributed to the decline and may result partly from the step changes referred to above. Because many more eggs are produced by older, larger fish than by younger ones, egg production (sum of abundance \times fecundity by age) followed a similar pattern to abundance of older fish, with a significant downward step in 1977-78 that explained 78% of the variance (Figure 2). This downward step can also be seen in the abundance of 6-mm larvae and in the YOY index, suggesting that it is not an artifact of the low precision of the Petersen estimates.

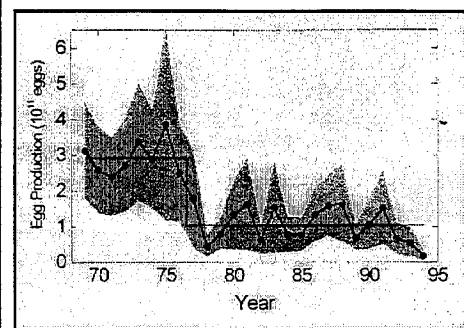


Figure 2. Time course of potential egg production as estimated by the Petersen mark/recapture estimate and age-specific fecundity, with 90% confidence limits (shaded). The thin line is a step function fit to the data ($r^2 = 0.78$, $p < 0.0001$, linear regression).

Flow Effects

Stevens (1977) reported a positive relationship between net delta outflow and an index of recruitment 3 years later. This relationship has apparently changed, and since about year class 1971 it is no longer statistically significant (Figure 3A). Furthermore, the Petersen estimate of abundance at

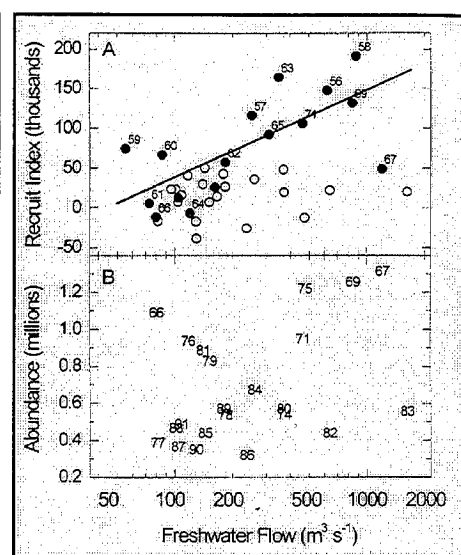


Figure 3. Recruitment vs. net delta outflow 3 years earlier. A, recruit index from the party boat fishery (Stevens 1977) with solid symbols for year-classes up to 1971 (shown by numbers), open symbols for subsequent year-classes, and a line indicating the significant regression for data up to year class 1971 ($r^2=0.46$, $p=0.002$, robust regression); B, Petersen estimate of abundance of 3-year-old striped bass; numbers are year-classes.

age 3 (essentially recruitment) is unrelated to flow 3 years earlier, either for the entire time series or for any early sequence of year-classes (Figure 3B). The failure of these relationships to hold could be due to effects of declining parental stock.

The egg-YOY survival index varied from year to year but had no time trend (Figure 4A). As previously reported (DFG 1987; Jassby *et al* 1995), this survival index is a function of flow conditions in the estuary. I calculated a regression of this index on X_2 and on the residuals from a nonlinear relationship of X_2 with exports. This linear regression was highly significant ($p < 0.0001$) and explained 59% of the variance in the log of the survival index. Based on more limited data on larval abundance and survival, most of the X_2 effect occurred by the time the larvae reached 6-mm length.

The YOY index was mainly a function of potential egg production, X_2 , and export flow. There was no indication of a decline in either egg-YOY survival or residuals from the model (Figure 4B). A downward trend might have been expected in 1988, because of the decrease in primary production and mysid abundance following the spread of the clam *Potamocorbula amurensis*. This indicates that, even at the currently low food levels in the estuary, variability in food does not seem to affect survival of young striped bass.

The analysis of recruitment data suggests that the relationship of striped bass production to flow conditions changed, perhaps in the early 1970s. However, since 1969 there has been no time trend in either the survival from egg to young-of-the-year or the portion of that survival not explained by flow conditions. This supports the contention that the decline in striped bass in the 1970s was not

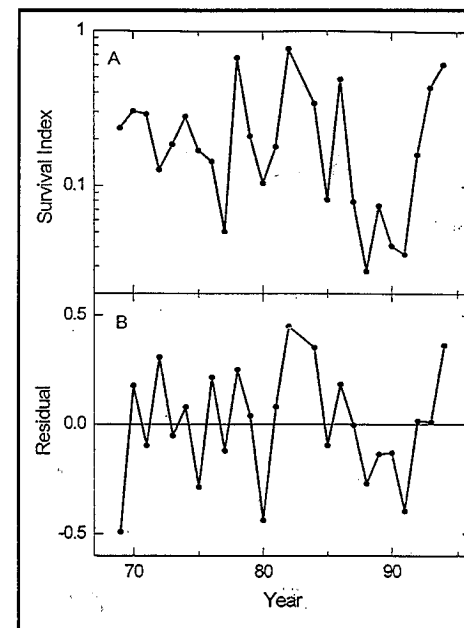


Figure 4. Index of survival from egg to young-of-the-year. A, time series of survival index (log scale); B, time series of residual from linear regression ($r^2=0.59$, $p < 0.0001$, linear regression on X_2 and the residual from a nonlinear relationship of export flow to X_2). Neither time series has a significant trend.

related to events occurring between spawning and the first summer of life.

Density Dependence

The relationship between the YOY index and recruits at age 3 (not including hatchery fish) was fitted to a Beverton-Holt saturating curve, indicating density-dependent survival (Figure 5A). At values of the YOY index above about 10-20, recruitment was independent of YOY index; at lower values, recruitment appeared to be positively related to YOY index.

Some would argue that a straight line would fit these data as well as the Beverton-Holt relationship. Although this may be true, a straight line does not make sense biologically. All of

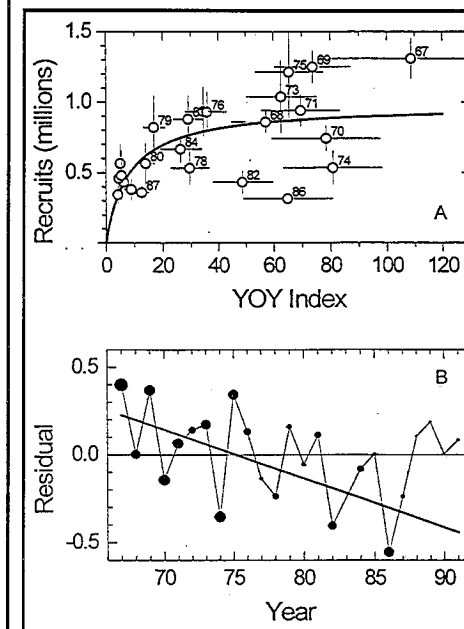


Figure 5. A, Relationship between YOY and recruitment at age 3 fitted to a Beverton-Holt stock-recruit curve:

$$\text{Recruits} = \frac{b \text{ YOY}}{a + \text{YOY}}$$

where $b = 0.98 \pm 0.11$ (standard error) and half-saturation constant $a = 8.1 \pm 4.0$ ($r^2=0.37$, $p < 0.001$, 22 df). Numbers are years, and horizontal and vertical lines give standard errors. B, time course of residual from A (line with symbols); sizes of symbols are scaled to the YOY index, and the straight line is fitted by linear regression weighted by the YOY index ($p < 0.002$, $r^2=0.35$).

the recruits were young-of-the-year 3 years earlier. If the YOY index were zero, there should be no recruits. Therefore, whatever line is fitted to these data must go through the origin, and to fit the data it needs to have a downward inflection. The Beverton-Holt curve does this, and has the added property of approaching an asymptote that we can interpret as carrying capacity of the environment for young (first summer to age 3) striped bass.

There is considerable scatter about the asymptotic part of the curve in Figure 5A, some of which is explained by a significant time trend in the residuals (Figure 5B). The residuals were weighted by the YOY index (represented by the size of the symbols) to emphasize variation around the asymptote, or carrying capacity. Carrying capacity has evidently been decreasing.

The combination of density-dependent survival between young-of-the-year and recruit with a declining carrying capacity helps to explain an anomaly apparent on comparing Figures 1 and 2. That is, if egg production declined with a step change in 1976-77, and YOY index follows egg production (although subject to flow effects), then why did abundance of age-3 fish not decline by a step change in 1979-80, and age 4 in 1980-81, etc.? The answer seems to be that recruitment was strongly dampened by density-dependent mortality and that the carrying capacity was declining independently of the step change in egg production.

Both the YOY index and the Petersen abundance estimate are highly variable, as suggested by the large error bounds in Figure 2 and the residuals in Figure 4. Therefore, I looked for independent corroboration of density-dependent mortality in young bass. I have found evidence of this

from three separate sources of data: the combined summer tow-net and fall midwater trawl data, and the San Francisco Bay Study midwater and otter trawl data. In these analyses, I used the raw data to calculate abundance as total population size for each survey. For the Bay Study data, I calculated an "apparent mortality" as the negative slope of abundance of age 0+ fish over time from July through April. For the combined summer-fall data, I fit a quadratic curve to the data and calculated the mean slope of that curve, since the mortality appeared to change linearly with time.

I refer to these estimates as "apparent mortality" because some of the decline in abundance within each year results from changes in catchability as the fish grow and disperse. I assumed that catchability did not vary systematically among years. A potential source of bias in the Bay Study data due to under-sampling the delta did not invalidate the results presented here. Apparent mortality rates from all three datasets were significantly, positively correlated with mean log abundance (Figure 6). This result does not arise as an artifact of

the analysis (slope and mean value are mathematically independent), but as a consequence of higher mortality when the population is large. This offers strong support to the contention that survival after the YOY index is set is density-dependent.

A consequence of this density dependence is that much of the variability in YOY index that is induced by X_2 and exports is eliminated. None of the three apparent mortality rates was related positively to X_2 ($p > 0.5$, 1-tailed test; correlations were actually negative) or to percent of the population estimated to be lost to export pumping (Table 1).

Survival from egg to recruit also had no time trend, and was related to X_2

Table 1. Correlations of estimated percent of biomass lost to export facilities vs. apparent mortality from three sampling programs.

Values given are Pearson correlation coefficients for each pair of values with 95% confidence limits.

Apparent Mortality from Sampling Program	Correlation with Estimated Mortality (Biomass)
Summer-Fall (YOY)	-0.06±0.43
Bay Study Midwater Trawl	-0.66±0.68
Bay Study Otter Trawl	-0.54±0.68

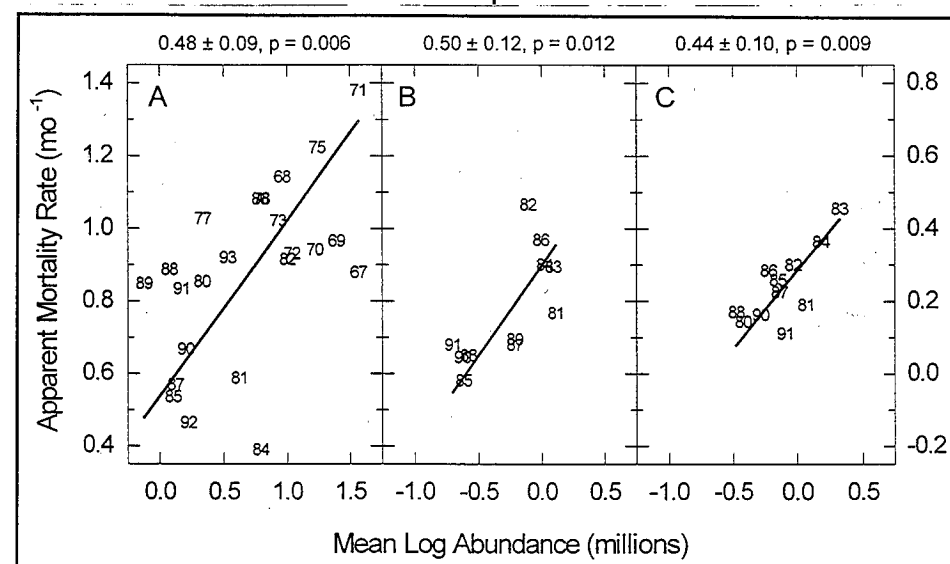


Figure 6. Apparent mortality rate plotted against mean log population size for: A, combined summer and fall surveys; B, Bay study midwater trawl; and C, Bay study otter trawl. numbers are years and lines give geometric mean regression slopes. Figures at the top are slopes ± standard errors for the geometric mean regressions, and p values for the correlations

and young-of-the-year with an interaction term (Figure 7). This interaction seems to work as follows: when X_2 is far landward (low flow), survival is poor. When X_2 is seaward, survival depends on young-of-the-year, with high survival only when the YOY index is low. This also indicates density-dependent survival and illustrates how density-dependence interacts with X_2 to influence recruitment.

The mechanism of this density dependence is unknown. Generally, mortality due to physical factors such as flow and exports is density-independent. Density dependence arises through biological mechanisms, principally competition for space, cannibalism, predator switching, or food limitation. Competition for space, probably the key density-dependent mechanism for salmon and reef fish, is unlikely for any pelagic fish. Cannibalism and predator switching could explain a density-dependent

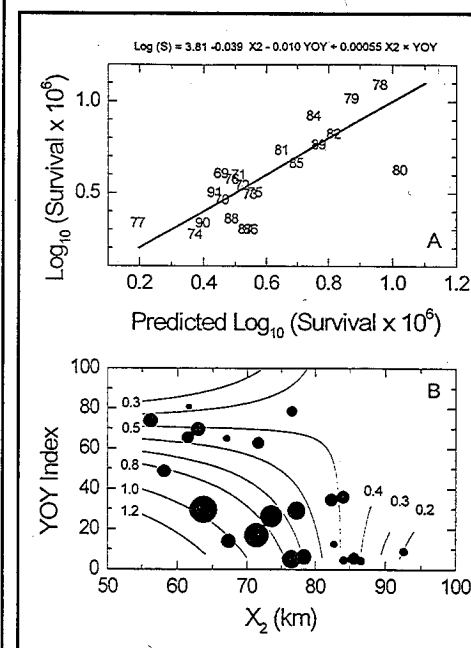


Figure 7. Survival from egg to recruit. A, Log of survival vs. that predicted from the a model including X_2 and YOY index (equation shown), with the 1:1 line. B, X_2 vs. YOY index with size of symbols representing relative magnitude of log egg-recruit survival, and contour lines of log survival determined by the model.

mechanism, but not the persistence of this mechanism into the post-decline period, or the decline in carrying capacity. Food limitation after the YOY stage seems a likely mechanism to explain both, given the long-term decline in chlorophyll and zooplankton abundance in the estuary, but I was unable to correlate the decline in carrying capacity with abundance of mysids, a major food item for age 0+ striped bass.

Why did the relationship of recruitment to flow collapse in the early 1970s? Part of the reason may be simply that attempting to analyze abundance as a simple, linear function of flow can only work if strong stock-recruit effects are absent. We have numerous examples (the "fish- X_2 " relationships; Jassby *et al* 1995) of straightforward relationships of abundance to flow in populations of short-lived fish, but for a long-lived population such as striped bass, that may not be appropriate. If carrying capacity for age 0+ fish was higher in previous years, the population may have been more often limited by density-independent factors such as flow conditions during early development or by density-dependent factors operating at another part of the life cycle.

Density dependence has been detected in other fish populations, but not in striped bass. That reflects the inherent variability in such populations, in which density-independent variability often swamps relatively subtle density-dependent effects. The data from the San Francisco estuary are probably the best and most complete for any striped bass stock. Without this large and extensive dataset, conclusions about density dependence and flow effects would be difficult if not impossible.

Conclusions

The decline in striped bass abundance over the last 2-3 decades appears to have been caused by a combination of increased adult mortality, particularly in fish over age 6, and declining carrying capacity for fish between their first summer and recruitment.

There is no convincing evidence that increasing exports, or decreases in survival during early life, caused the decline.

Interannual variability of recruitment once was but no longer is related to flow conditions in the estuary.

Survival of young bass is related to X_2 and export flows, but this variation is largely suppressed by density-dependent mortality after the first summer.

Acknowledgments

A more complete version of this report with several co-authors is being prepared for submission to a scientific journal. However, this article reflects my findings and opinions only, not those of my co-authors, reviewers, or funding sources. I gratefully acknowledge funding for this study by the California Urban Water Agencies and by the Interagency Ecological Program. I thank Lee Miller, Don Stevens, and Dave Kohlhorst for many discussions of these issues, insights, reality checks, and reviews, and for providing me with the data for this study. I thank the following people for their assistance in providing data or encouragement and for reviewing various versions of this work: Elaine Archibald, Randy Bailey, Bill Bennett, Randy Brown, Jim Buell, Jim Cowan, Phyllis Fox, Ed Houde, BJ Miller, Ken Miller, Joe Miyamoto, Bob Nuzum, Pete Rhoads, Kenny Rose, and Tom Taylor.

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